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Tommy J. Rauch  
*Louisiana State University*

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## Effect of Size and Prior Residence on Dominance in Male Seaweed Blennies, *Parablennius marmoratus*

TOMMY J. RAUCH

*Parablennius marmoratus* is a small bottom-dwelling blenny living on and around barnacles and other encrusting organisms on offshore petroleum platforms in the northern Gulf of Mexico. Males hold and defend cavities which provide cover and spawning sites. Aquarium tests were used to describe the effects of size and prior residence on dominance among adult male *P. marmoratus*. A size difference of 3 mm [ $\approx 5\%$  total length (TL)] was usually enough to enable a larger fish to control a single barnacle cavity. A size difference of 7 mm ( $\approx 10\%$  TL) always made a larger fish dominant. A prior resident was always able to defend his cavity for at least 10 min when challenged by a blenny of equal size. A prior resident was usually able to defend a cavity when challenged by a blenny 3 mm larger, but was displaced by a male 7 mm larger.

*Parablennius marmoratus*, the seaweed blenny, is a small demersal fish common on offshore petroleum production platforms in the Gulf of Mexico (Gallaway and Lewbel, 1982). Resident populations on natural substrata in the northern Gulf have been reported from the 7½-Fathom Reef east of Padre Island, Texas (Causey, 1969), and the Florida Middle Ground (Smith et al., 1975). Seaweed blennies have not been reported on the natural soft-bottomed substratum off the Louisiana coast. These cryptic blennies usually reside in barnacle cavities or hide among encrusting organisms growing on platforms. Barnacle cavities also provide spawning sites for these and other blennies on artificial reefs (Smith-Vaniz, 1980; Gallaway et al., 1981).

The bottom of the north-central Gulf of Mexico is composed mostly of river sediments and is characterized as a soft-bottom habitat (Hedgepeth, 1954; Gallaway and Lewbel, 1982). Each platform is a steel structure that extends throughout the water column and represents an island of hard substrate in this soft-substrata environment. Blennies inhabiting these artificial reefs possess no air bladder and have limited swimming ability (Nelson, 1994), so they spend their entire adult life on a single platform. Colonization of new areas is primarily by means of a pelagic larval stage (Peters, 1981). These "steel islands" have a finite amount of surface area available for habitation, so competition by these permanent demersal residents for suitable sites may be intense.

Offshore petroleum platforms function as artificial reefs and attract large numbers of fishes, including many predators (Sonnier et al., 1976). Fish aggregations found around ar-

tificial reefs are usually larger than those around adjacent natural reefs (Bohnsack et al., 1991). A cavity that provides a refuge from predation would be very important for survival in a predator-rich environment (Gallaway et al., 1981). Hastings (1991) has shown that chaenopsids spend more time within a cavity when in predator-rich habitats than when in sites experiencing low predation pressure.

Several investigators have described territorial behavior for members of the family Blenniidae. Nursall (1977, 1981) measured the sizes of territories and described the spawning habits of the redlip blenny in Barbados. The territorial interactions of several blennies in the Red Sea and waters off Australia were described by Roberts (1985, 1987). Ethograms have been provided for the agonistic behavior of *Blennius pholis* (Gibson, 1968) and the reproductive behaviors of several species of blennies (Abel, 1964; Marraro and Nursall, 1983). Observations on *Parablennius marmoratus* have shown that these fish defend certain cavities from conspecifics when placed in an aquarium (A. Bull, pers. comm.; pers. observ.). Studies of other blennies have used defense of a cavity as evidence of territorial behavior (Tavolga, 1958; Phillips, 1971a).

Dominance has been defined as a priority of access to resources (Kaufmann, 1983). Blenny dominance studies have examined traits such as size, sex, and prior residence that fish possessed when successfully holding territories. Phillips (1971b) used the number of aggressive displays to describe size and prior residence effects for *Chasmodes bosquianus*, a seasonal inhabitant of Chesapeake Bay. Prior residence rather than size was the most important determinant of dominance. Among juvenile *B. pholis*

(Gibson, 1968), size was the most important factor, but effects of sex and prior residence were not tested. Fishelson (1975) showed that the largest male was always dominant when several *Meiacanthus nigrolineatus* of both sexes were placed in an aquarium.

Size difference data were provided for interspecific dominance tests on two intertidal New Zealand fishes (Mayr and Berger, 1992). A 15% size difference is usually sufficient to affect the outcome of crustacean dominance contests (Shuster and Caldwell, 1989). No previous studies of blennies have related a percent size difference with factors that influence dominance. The access of dominant blennies to resources for shelter and spawning should increase their fitness (Kaufmann, 1983; Shuster and Caldwell, 1989; Mayr and Berger, 1992). Identifying factors affecting dominance will increase understanding of the abundance, size distribution, and use of space by demersal fish on artificial substrata.

Dominance studies of blennies are often restricted to males because in some species adult females do not hold territories (Phillips, 1971b, 1977). I examined the effects and interactions of size and prior residence on dominance of male *Parablennius marmoratus* inhabiting artificial reefs in the north-central Gulf of Mexico. The following questions were addressed: What intraspecific size differences are required to affect dominance? What intraspecific size differences affect the advantage of prior residence in these blennies?

#### MATERIALS AND METHODS

I caught seaweed blennies on 13 July 1993 at offshore petroleum platforms in South Timbalier Block 151 and on 9 Oct. 1993 at platforms in West Delta Block 117. Both areas are about 50 km off the Louisiana coast at water depths greater than 30 m. When caught, fish were located within barnacle cavities at depths between 10 and 17 m. I captured the blennies by using a zip-lock plastic bag (3.79 liters) that contained a soft plastic eyedropper (15 cm long). The opening of the plastic bag was held over a barnacle cavity containing a blenny. When the eyedropper was inserted into the barnacle cavity, the blenny swam out into the plastic bag. After the bag contained blennies, it was often held over another cavity, and the blenny inside the cavity came out, swam into the bag, and began displaying to the other blennies. Up to 20 blennies were caught on a single SCUBA dive with this method.

Males and females were separated using fea-

tures described by Smith (1974) and Smith-Vaniz (1980). I kept the blennies in 76- to 198-liter stock aquaria equipped with aquarium gravel, undergravel filters, and numerous small plastic tubes (1.6–1.9 cm diameter) for cover. An electric timer maintained a 12-h light-dark cycle. Water temperature (22–24 C) and salinity (32–35‰) approximated natural habitat conditions and were routinely monitored so the blennies could be moved from tank to tank without ill effects. The fish were fed Tetra Min flake fish food or frozen brine shrimp *ad libitum*, daily.

The blennies were acclimated for 4 d in the stock tanks before trials began, and all manipulations were completed within 5 wk of capture. Trials were run in 38-liter aquaria with undergravel filters and aquarium gravel. The tests were started 30 min after feeding, by which time the blennies had returned to typical nonfeeding behavior. I was not able to catch enough fish to complete these trials without using some fish twice. Therefore, in some cases one fish was used in both size and prior-residence trials. In these cases the blenny was acclimated in the stock tank for at least 3 d between trials.

The fish were measured to 1 mm [total length (TL)] by placing them on a prewetted plastic ruler. This procedure was checked by remeasuring some fish throughout the tests, and repeated measures never differed more than 1 mm. Previous dominance trials (Stephens et al., 1970; Phillips, 1971a, 1971b, 1977) and field manipulations (Kraak and Videler, 1991) for blennies and two intertidal fishes (Mayr and Berger, 1992) have used standard length or total length as a size measurement.

Behavioral descriptions follow Phillips (1971a), and unique behaviors of *P. marmoratus* are described below. Wallace (1987) predicted that a size difference of 10% should be perceived by combatants in nature. Differences of approximately 5–10% were used in these tests with seaweed blennies.

*Size trials.*—The effect of size on dominance was tested in a 38-liter aquarium separated into halves by a white plastic divider. Two male seaweed blennies were measured, and one was put on each side of the divider. The blennies could not see each other, and both were allowed to acclimate overnight. The next day the divider was removed and a barnacle was placed in the center of the aquarium. A cavity in the barnacle was big enough for one blenny to take cover, and each barnacle had only one

cavity suitable for these blennies. Observations were recorded every 10 min. for 30 min. and the fish that occupied the barnacle was scored as dominant. In some instances, a fish established dominance but continued to move around the aquarium. In these instances, the fish that initiated the greater number of attacks, and occupied the cavity between these attacks, was considered dominant. The fish that retreated from all or most attacks and attempted to occupy a location as far away as possible from the cavity in the aquarium was considered subordinate (Kaufmann, 1983). Also, the subordinate fish did not occupy the barnacle cavity. After 30 min, the fish were removed from the test tank and returned to the stock tanks.

Twenty tests included a 3-mm size difference between the larger ( $\bar{x} = 62.8$ ,  $SD = 4.43$ ) and smaller ( $\bar{x} = 59.8$ ,  $SD = 4.43$ ) blenny. The larger blenny was 4.2–5.5% longer than the smaller blenny for these tests. The same number of tests were run for a 7-mm difference, and the larger fish ( $\bar{x} = 65.95$ ,  $SD = 6.19$ ) was 8.8–13.5% longer in these tests. A chi-square test was used to evaluate the data against a null hypothesis of no size effect.

*Prior residence trials.*—The effect of prior residence was tested by measuring two blennies and placing one in a 38-liter aquarium with a single barnacle (described in *Size trials*). This fish was allowed to establish residence overnight, while the second blenny was put into a holding tank containing no shelter cavities. On the following day, the fish were fed, and only those blennies in the resident tanks that returned to the barnacle after feeding were used in tests. The second blenny (from the holding tank) was introduced to the test tank, and observations on dominance were recorded in the same manner as in size tests. After 30 min, both fish were removed from the test tank.

Twenty tests were run in which the prior resident fish was 7 mm smaller ( $\bar{x} = 59.85$ ,  $SD = 4.27$ ) than the introduced larger ( $\bar{x} = 66.85$ ,  $SD = 4.27$ ) fish, which gave the larger fish a 10.0–11.9% advantage in length. The same number of tests were run in which the prior resident fish was 3 mm smaller ( $\bar{x} = 61.9$ ,  $SD = 6.90$ ), and 20 tests were run in which the prior resident and the introduced fish were of equal size ( $\bar{x} = 63.2$ ,  $SD = 6.13$ ). The 3-mm size difference represented a 3.8–5.3% greater length for the introduced blenny.

A Cochran-Mantel-Haenszel (CMH) test was used to describe the effect of size in the prior resident tests. After the tests were completed,

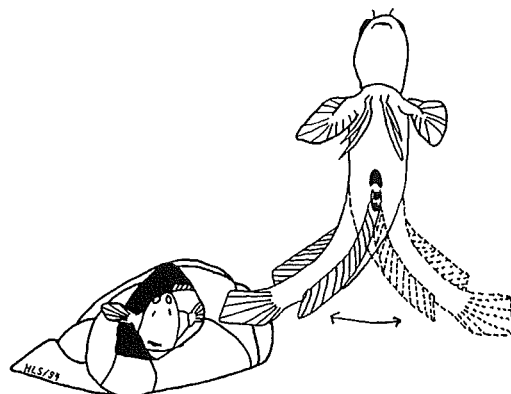


Fig. 1. Tail-dancing. The displaying blenny moves slowly in front of a conspecific while waving its tail from side to side slightly above the bottom.

the blennies were preserved and cataloged into the collection of fishes at the Museum of Natural Science at Louisiana State University. Seaweed blennies used in these tests include LSUMZ 10136 (6 specimens), 10339 (16), and 10340 (9).

## RESULTS

*Size trials.*—Size trials usually began with the blennies displaying, fighting for control, and entering the barnacle only after control was established. Common displays included fin-spread, mouth-open, and jaw-grip (Phillips, 1971a). Jaw-grip was a common behavior when one or both *P. marmoreus* were outside the enclosure (barnacle), although Phillips (1971a) observed this behavior for *C. bosquianus* only when one fish was inside the enclosure. Tail-dancing by *P. marmoreus* was a unique display (Fig. 1) and is described as a blenny exhibiting fin-spread while swimming with its tail slightly above the bottom. The lateral motion of the tail is exaggerated, and the displaying fish moves horizontally, one to several body lengths in front of the other blenny. After establishing dominance, a blenny entered the barnacle while the other blenny sometimes displayed (usually tail-dancing) for a few minutes before moving as far away from the dominant blenny as possible. In these trials, none of the larger fish was displaced once it controlled a cavity. The larger fish usually became more aggressive after gaining control of the cavity, and in one case removed part of the caudal fin of the smaller fish before they were separated.

Size was an important factor in both the 3-mm and 7-mm tests (Fig. 2). In all four trials in which the smaller blenny controlled the

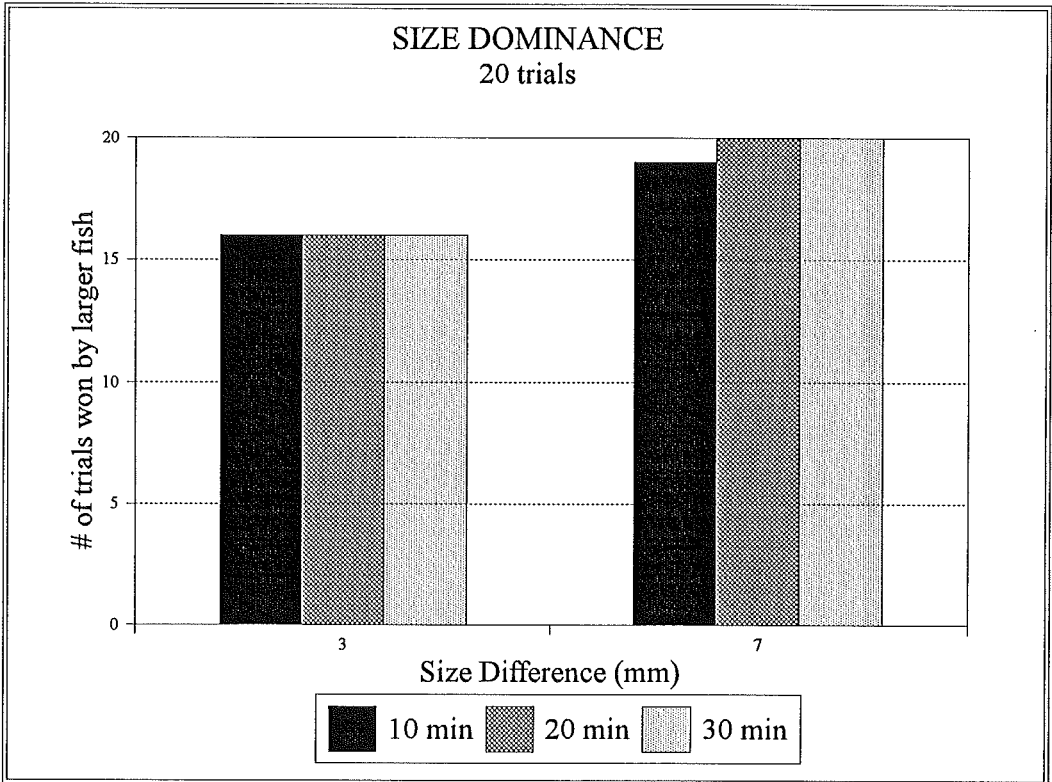


Fig. 2. Effect of size on competition for shelter (barnacle cavity) for 10-, 20-, and 30-min periods.

3-mm size dominance tests, the smaller blenny moved into the barnacle before confronting the larger fish. These four smaller blennies spent some time (1–10 min) in the cavity before they were challenged by the larger blenny. This short resident experience may partially account for the ability of smaller blennies to hold these barnacles.

Statistical analyses of the size tests are presented only for the 10-min reading; all readings after 10 min agreed with the 10-min reading. The 3-mm ( $\chi^2 = 7.2$ ,  $n = 20$ ,  $P = 0.00729$ ) and 7-mm ( $\chi^2 = 16.2$ ,  $n = 20$ ,  $P = 0.000057$ ) size differences gave the larger fish a significant advantage.

*Prior residence trials.*—Common displays of resident (smaller) fish that remained in the barnacle to confront the introduced fish included head-snap and mouth-open. Head-snap was displayed every time a male *P. marmoratus* approached another male in a barnacle, while Phillips (1971a) found this display more common for male–female encounters in *C. bosquianus*. Displays of the introduced (larger) fish included tail-dancing, fin-spread, and mouth-

open before approaching the barnacle. These trials resulted in jaw-grip if both blennies continued to contest dominance. Prior residents either remained in the barnacle or moved outside to engage in jaw-grip. When prior residents remained inside the cavity while confronting the introduced blenny, jaw-grip was always observed. Some prior residents that had been displaced displayed for several minutes (tail-dancing or fin-spread) before moving to the farthest corner of the aquarium. A blenny that had recently taken control of a barnacle displayed head-snap and mouth-open if the other male approached, and often left the barnacle to chase the other blenny around the aquarium. These chases were of short duration (1–5 seconds or once around the aquarium), and the dominant fish returned to the barnacle between chases. Once a prior resident was displaced, it was never able to reestablish control over a barnacle cavity within the 30-min test period.

Prior residence was important in the dominance of these fishes (Fig. 3). Among equal-sized *P. marmoratus* that had no other obvious differences, a prior resident was always able to

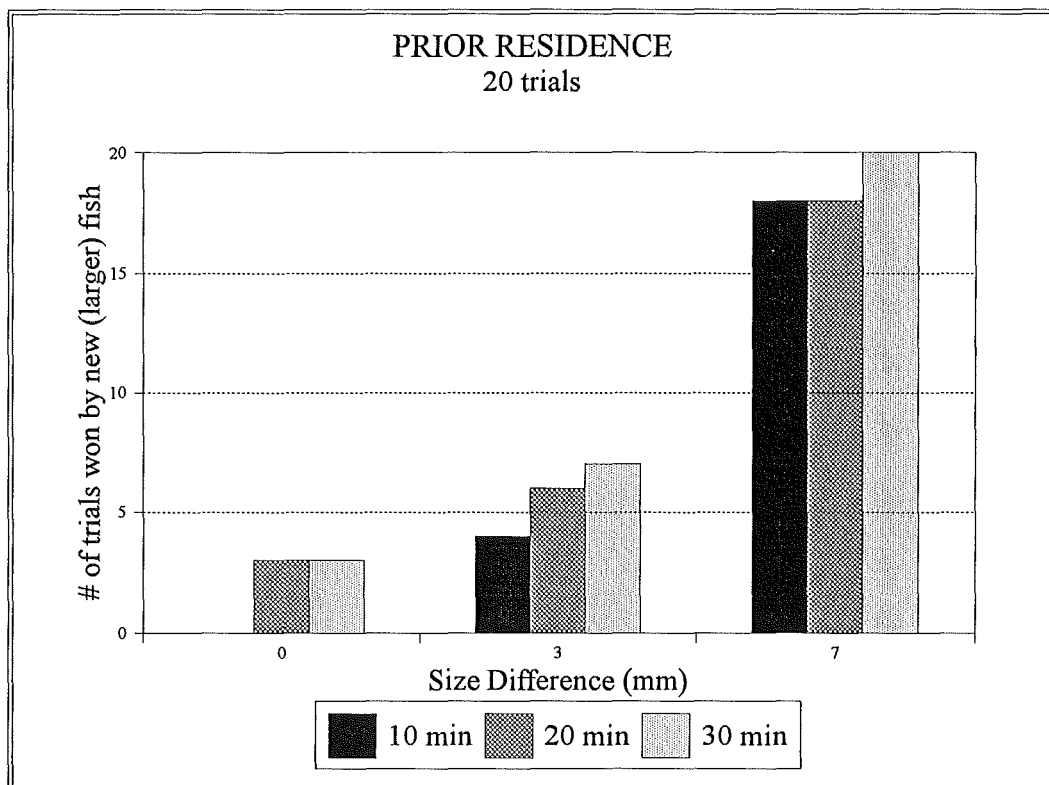


Fig. 3. Effect of prior residence on competition for shelter (barnacle cavity) for 10-, 20-, and 30-min time periods.

control a barnacle for at least 10 min. In relation to dominance, prior residence was usually more important than a 3-mm ( $\approx 5\%$ ) size difference, but this advantage was ineffective when the size difference was 7 mm ( $\approx 10\%$ ) or larger.

The results at 10, 20, and 30 min after the trials were started were used in the statistical analysis; there was a significant difference in the pattern of response of the dominance trials when fishes of different size classes (0%,  $\approx 5\%$ , and  $\approx 10\%$  size difference) were involved (chi-square analysis by CMH method = 88.1,  $P < 0.001$ ).

#### DISCUSSION

Blennioid fishes can be divided into two distinct groups according to type of territorial behavior, species in which both sexes hold territories, and species in which only males hold territories. Examples of blennies in which both sexes hold territories include *Ophioblennius atlanticus* (Nursall, 1977, 1981; Marraro and Nursall, 1983), *Meiacanthus nigrolineatus* (Fishelson,

1975), and *Exallias brevis* (Carlson, 1992). Only males hold territories in *Istiblennius zebra* (Phillips, 1977), *Hypsoblennius gentilis* (Stephens et al., 1970; Losey, 1976), and possibly *Scartella cristata* (Smith, 1974).

The *P. marmoreus* captured for these trials were 75–80% males. This suggests that seaweed blennies may be a species in which only males hold territories (and defend cavities). Females captured may have been exhibiting a predator avoidance mechanism (from the collector) and not defending these barnacle cavities.

Size appears to be the most important variable affecting dominance among male *P. marmoreus*. A size difference of 10% or more overcame the benefits of prior residence. This effect of size on dominance is consistent with data from Gibson (1968) for *Blennius pholis* and Fishelson (1975) for *Meiacanthus nigrolineatus*, two blennies which permanently inhabit a defined area. Seaweed blennies also inhabit a specific platform for their entire adult life. The only study (Phillips, 1971b) in which prior residence was shown to be more important than size in territorial dominance among blennioid

fishes involved the migratory blenny, *C. bosquianus*. Other factors, perhaps age or weight, not investigated in this study may also have an effect on the dominance of blennies.

Prior residence was important when the size difference was less than 10%. The effect of prior residence may be complicated in several ways. First, the presence of predators may limit the window of time available for a new fish to challenge a prior resident to short intervals. Large predators, such as jacks and groupers, are common around offshore production platforms (Hastings et al., 1976; Gallaway and Lewbel, 1982), and some are predators of blennies (Randall, 1967). A resident blenny challenged by a conspecific would retain control of the cavity if the challenger fell victim to predation. If challenges are limited to short durations, then prior residence may be a more important factor on platforms at sea than in aquarium tests. Second, other factors not examined in this study may enhance or detract from the advantage of prior residence. Resident *P. marmoratus* that remained in their cavity were often more successful in defending it than those which emerged to confront an introduced fish. This behavior may be acquired with experience, and therefore age may be an important factor. *C. bosquianus* usually leave their enclosures to confront intruders (Phillips, 1971b) in Chesapeake Bay. Phillips (1971b) suggested that a *C. bosquianus* that remains in an enclosure when confronting an intruder is on the defensive and would probably lose the enclosure if attacked by the other blenny (Phillips, 1971a). Increased predation pressure may select for seaweed blennies that remain in an enclosure when confronted by conspecifics on petroleum platforms.

The benefit of prior residence declined as the challenge for a cavity from a larger blenny continued for longer periods of time. This trend was most apparent in the prior-resident test with a 3-mm size difference. The effect of prior residence may be enhanced by environmental conditions (presence of predators), but it is not as permanent as the effect of one blenny having the advantage of larger size. Being larger conferred an advantage in these blennies that did not decrease in importance with time.

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